



Experimental reversal of soil acidification in a deciduous forest: Implications for seedling performance and changes in dominance of shade-tolerant species

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ABSTRACT

Acer saccharum Marsh. (sugar maple) and the less valuable *Fagus grandifolia* Ehrh. (American beech) are the dominant shade-tolerant canopy species over large forest tracts in northeast North America. Negative effects of soil acidification on sugar maple could favor greater dominance of beech in the “zero-sum game” dynamics of closed-canopy forests. A watershed-level Ca addition experiment, reversing some effects of acidification (including pH and Ca availability), provided an opportunity to test effects on beech and sugar maple seedling performance over 5 yrs, under different canopy species. Ca addition almost doubled leaf area of sugar maple and increased that of beech by over 40%. However extension growth was increased only in sugar maple. Both the direction of effects and the relative performance of maple and beech were consistent across canopy species. We combine our results and other evidence into a conceptual model of how soil acidification and Ca depletion is shifting the competitive balance in the seedling stage toward beech, implying an increase in beech relative abundance in the canopy, unless compensated by other factors, such as beech bark disease. These findings, and mounting evidence of other negative effects of soil acidification, suggest re-examination of the cost-effectiveness of chemical remediation in some poorly buffered forested watersheds.

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1. Introduction

Acidification of poorly buffered forest soils in northeastern North America leads to depletion of essential cations and increased availability of other, potentially toxic elements. These changes may be causing declines in sensitive species, and increases in species more tolerant of soil acidification. Specifically, there is concern that Ca depletion and Al toxicity may contribute to decline in *Acer saccharum* (Marsh.), sugar maple (Juice et al., 2006), and a concomitant increase in the much less valuable *Fagus grandifolia* Ehrh. (American beech) (Duchesne and Ouimet, 2009). For brevity, we refer to these species as maple and beech. At the Hubbard Brook Experimental Forest (HBEF) in New Hampshire USA, where soil acidification is well documented (Gbondo-Tugbawa and Driscoll, 2003), Ca was added to an entire watershed in 1999 to experimentally reverse some of the changes due to soil acidification, and to test ecosystem and organism responses (Cho et al., 2010). Tree species that respond most positively to the experimental Ca addition should be those that suffer most from acidification and Ca

depletion, and would benefit most from reduction in air pollution that drives soil acidification. This logic is central to the development of this paper.

At the HBEF, in samples taken at similar elevation to our study site, the forest is heavily dominated by maple (33%), yellow birch (*Betula alleghaniensis*, 29%) and beech (23%), where percentages refer to total above and below ground biomass, calculated from data in Siccama et al. (2007). In this paper, we focus on maple and beech, which have similar shade-tolerant life-histories, and occur as the late successional co-dominants over large tracts of eastern North America (Braun, 1950). Their competitive balance in beech–maple forests has been the focus of numerous theoretical and empirical studies (reviewed in Takahashi et al., 2010). In closed-canopy forests, the dynamics of competing canopy species are constrained by available canopy space, such that losses in canopy dominance by one species are balanced by gains in other species (sometimes described as a “zero-sum game”).

Fig. 1 represents a logical and empirical framework to assess the consequences of soil acidification for changes in the relative success of maple and beech in gaining canopy dominance. Fig. 1A shows hypothesized effects (in pale gray) of reversal of acidification that would increase the overall performance (establishment, growth and survival) of maple relative to beech. The results of testing such hypotheses then determine the inferences (Fig. 1B)

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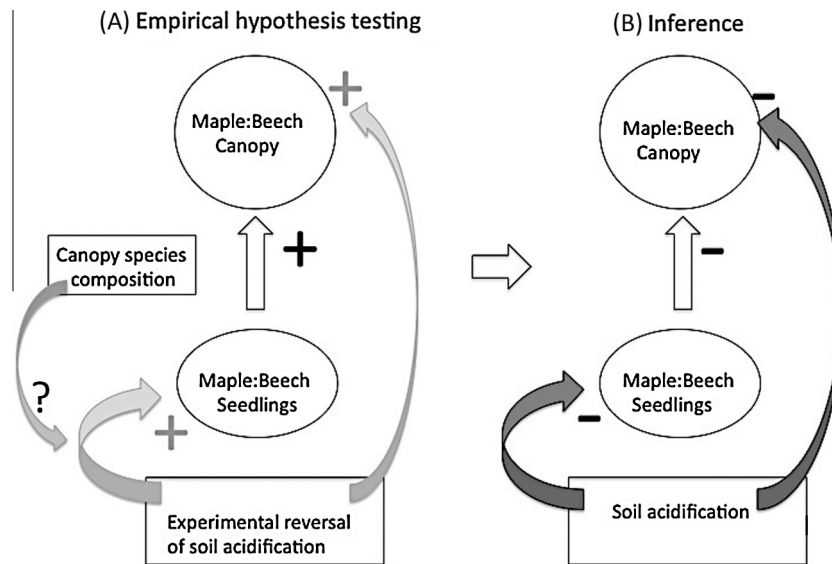


Fig. 1. Hypotheses and inferences, regarding effects of soil acidification on the relative performance of sugar maple and beech at Hubbard Brook Experimental Forest (HBEF), NH. Figure includes information from the literature as well as findings from this study. Maple:beech represents performance of maple relative to beech, in the canopy and seedling layers (see details in text). Pale gray, filled arrows on left (A) represent hypotheses. Dark gray, filled arrows on right (B) represent inferences from testing those hypotheses. Black, unfilled arrows in both A and B represent logical connections: increased (relative) maple performance at the seedling stage leads to higher (relative) recruitment of maple to the canopy, unless compensatory trends occur between seedling and canopy stages. Black, unfilled arrow in center connects the testing of effects of reversal of soil acidification (on left, A), with inferences (on right, B) regarding anthropogenic soil acidification effects. Reversal of soil acidification enhanced relative performance of maple both in seedlings (this study and evidence from literature) and in the canopy (evidence from literature). Effects of reversal of acidification on maple:beech seedling performance did not depend on the identity of the canopy species above (this study), so Canopy Species Composition is omitted from inferences on right (B). Overall, findings from this and other studies imply that soil acidification is reducing maple dominance relative to beech.

regarding the effects of anthropogenic soil acidification on the relative dominance of maple and beech.

If reversal of soil acidification increases the seedling performance of maple relative to beech (Fig. 1A, lower left, gray “+” arrow), the representation of maple relative to beech in the canopy would be increased (center, black unfilled “+” arrow) unless compensatory trends occur between the seedling and canopy stages. A potential complicating factor (left gray arrow, marked “?” because there is no *a priori* directional hypothesis) is that the species of canopy tree dominating a local area could influence whether and how Ca addition to the soil affects the seedling performance of beech and/or maple seedlings under its canopy. The empirical research in this paper addresses these hypotheses (lower two gray arrows in Fig. 1A).

Reversal of soil acidification can also affect canopy trees directly: the right, gray “+” arrow in Fig. 1A represents the hypothesis that Ca addition favors the performance of canopy maple relative to canopy beech. In Section 4, we summarize the evidence from original research from this study, along with other relevant evidence from the HBEF and other northern hardwood sites, to assess the support for the hypotheses in Fig. 1A (reversal of soil acidification, all three gray arrows). On that basis, we develop inferences regarding the effects of anthropogenic acidification of forest soils in northern hardwood forests on the competitive balance between maple and beech (Fig. 1B).

In the remainder of Section 1, and in Sections 2 and 3, we focus on testing the hypothesis that reversal of soil acidification favors maple seedlings relative to those of beech. To do so, we compare the seedling performance (focusing on extension growth and growth in leaf area) of maple and beech, in both Ca-added and control sites.

Further, we test whether the performance of seedlings depends on which species occupies the canopy above them. The species of canopy tree dominating a local site influences the quantity and quality of litter on the forest floor and key aspects of nutrient dynamics, as demonstrated for northern hardwoods forest by

Finzi et al. (1998) in a study that included both beech and maple. There is also evidence from northern hardwood forests that the species identity of a canopy tree results in plant-soil feedbacks via soil biota under its canopy, which in turn can drive strong species-specific effects on seedling performance (McCarthy-Neumann and Ibáñez, 2012). Thus, to evaluate the implications of seedling performance for canopy replacement and forest dynamics, it is important to test whether the seedling performance of maple relative to beech differs under different canopy species. Specifically, we test whether canopy species identity influences the response of seedlings to Ca addition, which would manifest as a significant interaction between canopy species and Ca treatment. To date, research on the effects of soil acidification (and partial reversal of those effects via Ca addition) on seedling performance have not included assessment of canopy species effects.

For maple, the most abundant species, with known sensitivity to soil acidification, we tested seedling performance under canopy trees of all four of the most abundant canopy species at our research site, i.e. yellow birch and white ash (*Fraxinus americana*), in addition to the focal species, maple and beech. For beech seedlings, for which previous research leads to the expectation of little or no effect of Ca addition, we focus on the beech–maple interaction, comparing beech seedling performance under beech and maple canopies.

2. Methods

The HBEF is an intensively studied northern hardwoods forest in the White Mountains of the northeastern USA, described in detail in Likens and Bormann (1995). Several drainage basins within the HBEF have been designated as experimental watersheds and identified by numbers (e.g. Watershed 1). In 1999, a slow-release form of wollastonite (CaSiO_3) was applied aerially at $0.85 \text{ Mg Ca ha}^{-1}$ to the entire Watershed 1 (Peters et al., 2004). The substantial increases in pH and Ca content in the forest floor, which apparently peaked in 2002–2004, are described in Groffman et al. (2006) and

Cleavitt et al. (2011). The present study was conducted in the low-elevation part of Watershed 1 (480–587 m asl) where the forest was heavily dominated by hardwood species, and in a control site defined as the area in the same elevational range, between Watershed 1 and the nearby Watershed 2. (Watersheds 1 and 2 share a common boundary in their upper elevations.) Both Ca-added and control sites were ca. 3.5 ha in area.

We randomly selected 34 canopy trees (defined as those with >70% of their crowns in the main canopy layer, as estimated visually from below), in each of the Ca-added and control areas, by overlaying random-point grids on detailed maps. We excluded trees that were within 5 m of obvious openings in the canopy, i.e. tree-fall gaps and streams. The abundances of canopy trees species did not differ significantly (χ^2 test) between our samples in the Ca-added and control areas.

To control for seedling age and to maximize comparability between the seedling species, we took advantage of a mast-seeding event for both maple and beech in 2002 that produced seedling cohorts in 2003. We measured only these 2003 cohorts, which at the time of sampling dominated the seedling layer in both the Ca-added and control areas. On all such maple and beech seedlings under the projected crowns of the sampled canopy trees ($n = 447$ maple and $n = 369$ beech seedlings, all <25 cm tall), we measured extension growth for the five-year period 2003–2007 inclusive. We also quantified leaf area per seedling, by flattening each leaf between glass plates containing a linear scale, imaging with a Canon PowerShot A85 camera, digitizing, and calculating leaf area using ImageJ software (Rasband, 2007).

We used mixed-model ANOVAs in SAS 9.2 for analysis of seedling responses (leaf area and 5-yr extension growth), with Ca treatment and canopy species as fixed effects, and individual canopy trees (nested within treatment) as a random effect. Individual seedlings were nested within canopy trees. Data were log-transformed to satisfy normality assumptions. We used residual maximum likelihood and Wald Z-tests for covariance parameters, and the containment method for denominator degrees of freedom in tests of fixed effects. Model selection was based on AIC values; non-significant effects were omitted in the final models. Results were robust to choices among alternative estimation methods.

3. Results

Because the seeds of beech are much larger than those of maple, with greater seed reserves, seedlings of beech (of the same age and under the same conditions) are also much larger than those of maple. Hence, we focus on the changes in leaf area and growth (Ca addition vs. controls) for each species, rather than on the magnitudes of those responses. We first report the effects of Ca addition on sugar maple seedling performance, under the four main canopy species. Then we focus on implications of Ca addition for changes in the relative seedling performance between the two dominant shade-tolerant canopy species, maple and beech.

Ca addition almost doubled leaf areas in 5-yr-old maple seedlings (95% increase compared to controls, averaged over all four species of canopy trees, Fig. 2A). Increases in maple extension growth due to Ca addition were also substantial (25% increase, averaged over canopy tree species, Fig. 2B). Both increases were highly significant (leaf area $F_{1,41} = 23.9$, $P < 0.0001$; extension growth $F_{1,41} = 23.1$, $P < 0.0001$). Effect sizes, using Cohen's d , which takes both the difference in means and variability into account, were 0.647 for leaf area and 0.761 for extension growth. The increases in maple seedling performance with Ca addition were not dependent on canopy species, i.e. there was no significant treatment X canopy species interaction, for either leaf area or extension growth in maple seedlings.

Like maple, beech 5 yr-old seedling leaf area was increased substantially by Ca addition ($F_{1,21} = 8.9$, $P = 0.007$). But the increase in beech leaf area was less than for sugar maple, a 43% increase over controls, averaged over canopy species (Cohen's $d = 0.442$, Fig. 2C). Beech seedling leaf area was significantly higher under canopy beech than under maple, irrespective of Ca treatment (significant main effect of canopy species; $F_{1,326} = 4.23$, $P = 0.041$). Unlike maple, beech seedling growth was not increased by Ca addition (Fig. 2D).

As for maple, there was no significant treatment X canopy species interaction for leaf area or growth responses, i.e. even though there was evidence (in beech) for a canopy species effect on seedling performance, the effects of Ca addition did not depend on canopy species.

4. Discussion

4.1. Findings of this study

Several strong patterns emerge from the results. First, our finding of a 95% greater leaf area in the Ca treatment after 5 yrs of growth for the 2003 cohort shows that the effects of Ca addition on sugar maple seedling performance remained strong 8 yr after the watershed-level pulse experiment. The leaf area and growth responses of maple seedlings in our results are even greater than those found in the earlier post-treatment years by Juice et al. (2006), who reported 50% higher leaf biomass due to the Ca treatment for the 2003 maple cohort in the first year of growth, and 65% increase in the second year (these increases in leaf biomass were due to an increase in leaf area, since leaf mass per unit area was not affected). Further, we found that maple seedling extension growth increased by 25% due to Ca treatment over the period 2003–2007, compared to the results of Juice et al. (2006) who found no Ca-addition effects on height of the 2003 cohort (in their first year of growth), and only a 13.5% increase by the end of the second year. This extended response of sugar maple seedling response, into the eighth year after the 1999 watershed-level Ca addition, is in spite of evidence that the effects on pH and foliar Ca peaked around 2002–2004 at the HBEF (P. Groffman, unpublished data, cited in Cleavitt et al., 2011). However, a more recent analysis (Cho et al., 2012) found that acid neutralization by the Ca treatment remained strong 6 yrs after application and concluded that wollastonite addition is an effective long term mitigation strategy for reducing the harmful effects of soil acidification in northern hardwoods. In a longer-term liming experiment in Quebec, dolomitic lime application to sugar maple trees had persistent effects on soil chemistry, and continuing positive effects on sugar maple tree growth and condition 15 years after liming (Moore et al., 2012).

Second, even though canopy species identity influences both local nutrient dynamics (Finzi et al., 1998) and soil biota, which can have species-specific effects on seedling performance (McCarthy-Neumann and Ibáñez, 2012), the Ca enhancement of maple seedling performance occurred across canopy species. This implies that soil acidification has reduced maple seedling success throughout this northern hardwood forest.

Third, the performance of beech, the species considered most acid-tolerant in northern hardwoods forests, and least sensitive to Ca limitation (Minocha, 2010), was also enhanced by Ca addition at the seedling stage. This result is contrary to expectations based on evidence from adult beech (e.g. Long et al., 2011). However, it is consistent with results of Kobe et al. (2002), who found that liming of transplanted beech seedlings increased their foliar Ca concentration. Our results indicate that even beech has been substantially

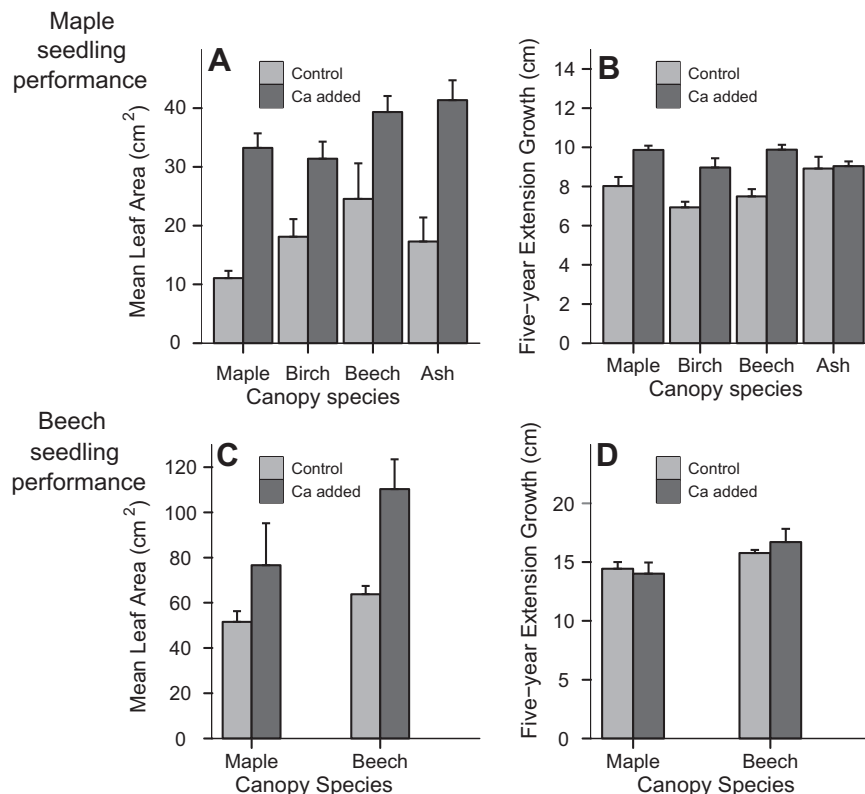


Fig. 2. Response of sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.) seedlings to experimental calcium treatment, and to the species of canopy tree above, at the Hubbard Brook Experimental Forest, NH, USA. Leaf areas and 5-yr extension growth (2003–2007) were measured in 2008 on 2003 seedling cohorts of each species, following a watershed-level calcium addition experiment in 1999. Canopy species are sugar maple, yellow birch (*Betula alleghaniensis*), American beech, and white ash (*Fraxinus americana*). A. Sugar maple seedling leaf area. B. Sugar maple seedling extension growth. C. American beech seedling leaf area. D. American beech seedling extension growth. Bars are ± 1 S.E.

and adversely affected in its seedling performance by soil acidification.

However, the lack of response to Ca addition in beech extension growth, in spite of substantial increases in leaf area, indicates a markedly different allocation pattern in beech: investment in extension growth appears to be a lower priority than for maple, at least in the understory conditions represented by our data. We suggest that beech and maple may have different physiological responses to increased Ca availability, which then in turn influence resource allocation. Ca is involved in complex signaling pathways in plants, and as a consequence Ca limitation may affect detection of and responses to environmental conditions, including light availability (Schaberg et al., 2001). Such mechanisms may influence the allocation of resources to leaf, stem and root. The findings of Zaccherio and Finzi (2007), in a northern hardwood forest in Connecticut, are consistent with this hypothesis: fertilization with Ca increased beech seedling growth much more in understory conditions than in canopy gaps. If changes in Ca-mediated regulatory mechanisms are operating in the seedlings we sampled, it is unlikely that maple and beech would respond identically to Ca addition, and the evidence suggests that they differ.

Fourth, focusing more sharply on the interactions between maple and beech, the two shade-tolerant canopy species that compete for dominance, we can infer that seedling performance of maple has been more compromised by soil acidification than that of beech. This is apparent in the greater enhancement of leaf area by Ca treatment in maple seedlings compared to beech, and in the significant increase in extension growth that occurred only in maple seedlings.

In another study in Quebec, a thorough analysis of static data (age structure and radial growth of surviving beech and maple

saplings) showed a decline in maple radial growth with concomitant increase in growth of beech over the period 1965–2000, but associated these trends with size and suppression status of individuals, rather than with spatial variation in current soil base status (Gravel et al., 2011). The authors suggest that evidence for changes in the relative recruitment dynamics of these species must be sought in survival, rather than growth data. However, the weight of evidence from survival, growth and seedling densities, from this paper and those cited in Sections 1 and 4, strongly indicates that soil acidification has decreased maple seedling performance success relative to that of beech. The relative dominance of beech and maple can vary with edaphic conditions in beech–maple forests (Takahashi and Lechowicz, 2008) and it is therefore likely that the magnitude of effects of soil acidification (and of experimental reversals using Ca treatment) vary spatially. However there is, to our knowledge, no evidence to suggest that any soil conditions could cause beech to be more sensitive to soil acidification than maple in the seedling stage.

Unless other factors compensate, the evidence implies a trend toward increasing beech abundance, relative to maple. The infection of beech in northern hardwoods forest by beech bark disease (BBD) is clearly a potential compensating factor. One would expect the effects of BBD, which was widespread in the HBEF by the early 1970s (Siccama et al., 2007) and has reduced beech radial growth in New Hampshire (Gavin and Peart, 1993), to reduce beech's overall competitive ability. Yet beech has remained abundant in diseased "aftermath" forests, including the HBEF, both in the canopy (Siccama et al., 2007) and in the understory (Holmes and Sherry, 2001). While high densities of beech sprouts (clonal reproduction) are associated with the spread of BBD (Houston, 1975), recent work at the HBEF shows that this is not a direct consequence of

the disease at the level of individual parent trees: clonal reproduction by beech is actually least prolific in the most diseased canopy beech, and greatest in trees with few or no disease symptoms (Wheat et al., unpublished data). Thus, the high densities of beech sprouts appear to be a consequence of root disturbance and increased light penetration, i.e. effects of BBD appear to be indirect, mediated through canopy dieback and perhaps root disturbance related to the fall of coarse woody debris associated with tree and branch mortality. The increase in beech seedling and sapling densities with the advent of BBD reduces maple seedling survival (Hane, 2003) through direct interactions, largely due to shading by beech saplings. We did not in this study attempt a comprehensive evaluation of how BBD has altered beech population dynamics. Apart from sprout reproduction, BBD has almost certainly reduced the survival of juveniles to (and persistence in) the canopy. Reductions in growth due to BBD (Gavin and Peart, 1993) inevitably increase transit time of individuals, and thus reduce their cumulative probability of survival over the period required to attain canopy dominance.

Our findings do include some of the influences of BBD, via the current condition of beech canopies, which can influence both beech and maple seedling performance. The greater leaf area of beech seedlings under conspecific beech canopies than under maple (Fig. 2C) was statistically significant. Maple seedling leaf area followed the same trends as for beech, i.e. seedling performance was higher under beech than under maple (Fig. 2A). While the main effect of canopy species was not significant in that analysis, when tested across all canopy species (see Results), the special focus on the two late successional co-dominant shade tolerant species justifies a second analysis of the maple data in Fig. 2A, parallel to that for beech, i.e. including the data for maple seedlings under beech and maple canopies only. In this reduced analysis there was a significant main effect of canopy species on maple seedling leaf area, i.e. greater seedling performance under beech than under maple ($F_{1,222} = 5.6$, $P = 0.019$). That both species regenerate better under beech may be due to the thinning of beech canopies resulting from beech bark disease.

Because our results imply a shift in the relative performance of beech and maple toward beech in the seedling stage with soil acidification, this shift should tend to increase the relative abundance of beech in the canopy, unless the negative effects of BBD on the later stages of the beech life cycle compensate for the shift toward beech in the seedling stage. Because of the long transit time to the canopy from the seedling stage, it may take several more decades for the full consequences of acidification-induced changes in relative seedling performance to play out in terms of canopy dominance. But the enhancement of the relative success of beech seedlings due to acidification may be partly responsible for the persistence of beech relative abundance in the canopy of northern hardwoods forests even several decades after the arrival of the killing front of BBD.

4.2. Synthesis of findings from this study and from the literature

As developed above, our findings strongly support the hypothesis (lower gray arrow in Fig. 1A) that reversal of soil acidification favors the performance of maple seedlings relative to beech. This conclusion was robust to the spatial mosaic in seedling environments resulting from the individual canopy trees of different species. Several other studies provide evidence consistent with our findings at the seedling stage, although none includes the effect of canopy species. Focusing on maple seedlings, Juice et al. (2006) documented higher densities, early survivorship and biomass following Ca addition at the HBEF. The findings of Cleavitt et al. (2011) were consistent with those of Juice et al. (2006), although maple seedlings transplanted to Ca-enriched soils in

2006 showed less positive effects, possibly due to reduced effects of the Ca treatment over time. Positive effects on maple seedling radial growth and survival were also found in a separate Ca addition experiment at the HBEF (Kobe et al., 2002). Data on beech seedling performance are more limited but also consistent with our results. Experimental liming at the HBEF did not significantly increase radial growth of transplanted beech seedlings (Kobe et al., 2002), in spite of increased foliar Ca concentrations. Liming of soils in Quebec resulted in higher maple seedling densities, both in absolute terms and relative to other species, especially beech (Moore et al., 2012). Recent work by Duchesne et al. (2013) showed that liming in Quebec increased the basal area growth of maple saplings twofold, with no significant effect on beech.

Taken together, our findings and those from the literature strongly support the inference (lower black arrow in Fig. 1B) that anthropogenic soil acidification has shifted the relative performance of seedlings and saplings in favor of beech over maple. In the absence of compensating factors, these dynamics result in a shift in canopy dominance in favor of beech (center block arrow in Fig. 1B, negative influence on maple:beech ratio).

Evidence from the literature also supports the hypothesis (right gray arrow in Fig. 1A) that reversal of soil acidification has direct positive impact on the growth and condition of canopy maple trees, relative to those of beech. Following Ca addition, there is clear evidence for a positive radial growth response in maple canopy trees at HBEF (Juice et al., 2006; Huggett et al., 2007), in Pennsylvania (Long et al., 2011) and in Quebec (Ouimet et al., 2008; Moore et al., 2012). Similarly, reversal of acidification had positive effects on maple canopy tree crown vigor at the HBEF (Juice et al., 2006; Huggett et al., 2007) and in Quebec (Moore et al., 2012). Less is known about the response of canopy beech to reversal of acidification, but long term liming had no effect on canopy beech radial growth in Pennsylvania (Long et al., 2011). Thus, available evidence supports the inference (right black arrow, Fig. 1B) that anthropogenic soil acidification has reduced the performance of maple canopy trees relative to beech.

Overall, therefore, there is strong evidence that anthropogenic soil acidification is shifting the competitive balance in beech–maple forests toward greater beech dominance. Soil acidification may have been altering regeneration dynamics for several decades, but the effects on canopy dominance would be expected to play out over even longer time scales, due to the longevity of canopy trees. Increase in beech abundance relative to maple implies substantial reduction in the economic value of northern hardwood forests. These findings, along with mounting evidence of other negative effects of soil acidification, suggest a re-examination of the cost-effectiveness of chemical remediation in some poorly buffered forested watersheds.

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